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Growth dynamics of root and shoot hydraulic conductance in seedlings of five neotropical tree species: scaling to show possible adaptation to differing light regimes

Abstract The dynamics of growth (shoot and root dry weights, surface areas, hydraulic conductances, and root length) were measured in seedlings of five neotropical tree species aged 4–16 months. The species studied included two light-demanding pioneers (*Miconia argentea* and *Apeiba membranacea*) and three shade-tolerant young- or old-forest species (*Pouteria reticulata*, *Gustavia superba*, and *Trichilia tuberculata*). Growth analysis revealed that shoot and root dry weights and hydraulic conductances and leaf area all increased exponentially with time. Alternative methods of scaling measured parameters to reveal differences that might explain adaptations to microsites are discussed. Scaling root conductance to root surface area or root length revealed a few species differences but nothing that correlated with adaptation to light regimes. Scaling of root surface area or root length to root dry weight revealed that pioneers produced significantly more root area and length per gram dry weight investment than shade-tolerant species. Scaling of root and shoot hydraulic conductances to leaf area and scaling of root conductance to root dry weight and shoot conductance to shoot dry weight also revealed that pioneers were significantly more conductive to water than shade-tolerant species. The advantages of scaling hydraulic parameters to leaf surface area are discussed in terms of the Ohm's law analogue of water flow in plants.

Key words Hydraulic conductance · Root · Shoot · Growth dynamics · Neotropical tree seedlings

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Introduction

A number of studies have focused on the hydraulic architecture of large woody tropical plants, e.g., trees, shrubs, and vines (see for example, Ewers et al. 1991; Patiño et al. 1995; Tyree and Ewers 1996). Parameters measured generally have been confined to hydraulic conductance of woody shoots. The basic approach entails measuring the hydraulic conductivity of excised stem segments (K_h = water flow rate per unit pressure gradient) of different diameters to obtain a regression of K_h versus diameter. Hydraulic maps of large trees, shrubs, or vines have been used to deduce xylem water potential drops within the woody crown based at representative evaporative flux densities (E) from leaves and the K_h versus diameter regressions. The K_h values have been scaled by dividing them by the cross-sectional areas of stems to yield specific conductivities, K_s, or by dividing them by leaf area distal to the stem segment to yield values of leaf specific conductivities, K_L. Rapidly growing pioneer species have larger K_L and/or K_s values than slower-growing species (Tyree et al. 1991; Machado and Tyree 1994). This has been interpreted in terms of the need of plants to have high levels of water potential (Ψ) to achieve high relative growth rates in meristems.

Little is known about the differences in total root conductance of tropical plants relative to shoot conductances. Are values of hydraulic conductance of seedlings higher in pioneer species than in slower-growing shade-tolerant species? Studies of root architecture and hydraulic conductivity are especially needed for shade-tolerant species since seedlings of these species are likely to experience conflicting demands upon their dry mass allocation (Burslem 1996). Whereas low irradiance conditions tend to increase the relative proportion of dry mass invested as leaves and shoots (Björkman 1981), low soil moisture availability leads to an increased mass allocation to roots (Bradford and Hsaio 1982). Studies of root morphology and physiol-

ogy, and the influence of roots on water relations is underrepresented for tropical seedlings. Furthermore, resource allocation patterns to roots are usually interpreted as response to the light environment (Garwood 1996).

The recent development of a high-pressure flowmeter (HPFM) (Yang and Tyree 1994; Tyree et al. 1995) allows the rapid measurement of root and shoot hydraulic conductance of seedlings. Thus, it is now possible to study the growth dynamics of seedlings while monitoring dynamic changes in hydraulic conductance of roots and shoots. This ability raises the question of how best to scale conductance parameters to reveal ecological adaptation to light regimes. More thought has gone into scaling of shoot parameters (Tyree and Ewers 1996) than root parameters so a review of arguments for roots seems appropriate.

Root conductance (K_r) can be defined as water flow rate (kg s^{-1}) per unit pressure drop (MPa) driving flow through the entire root system. Values of K_r could be scaled by dividing by some measure of root size (root surface area, total root length, or mass) or by dividing K_r by leaf surface area. Division by root surface area (A_r) is justified by an analysis of axial versus radial resistances to water flow in roots. In the radial pathway, water flows from the root surface to the xylem vessels through non-vascular tissue. In the axial pathway, water flow is predominately through vessels. The resistance of the radial path is usually more than that of the axial path (Frensch and Steudle 1989; North et al. 1992). Most water uptake is presumed to occur in fine roots (<2 mm diameter) and fine-root surface area is usually >90% of the total root surface area (personal observation). So root uptake of water would appear to be limited by root surface area and hence it is reasonable to divide K_r by A_r yielding a measure of root efficiency. Some roots are more efficient than others. Division of K_r by total root length (L) is not as desirable, but is justified because A_r and L are correlated approximately and L can be estimated by a low-cost, line intersection technique rather than a high-cost, image analysis technique.

Scaling by root mass is justified by consideration of the cost of resource allocation. Plants must invest a lot of carbon into roots to grow and maintain them. The benefit derived from this carbon investment is enhanced scavenging for water and mineral nutrient resources. Total root dry weight (TRDW) is a measure of carbon investment into roots. Thus the carbon efficiency of roots might be measured in terms of K_r/TRDW, A_r/TRDW, or L/TRDW. Scaling by TRDW provides information of ecological rather than physiological importance.

Scaling of K_r by leaf surface area (A_L) provides an estimate of the 'sufficiency' of the roots to provide water to leaves. The physiological justification of scaling K_r to A_L comes from an analysis of the Ohm's law analogue for water flow from soil to leaf (van den Honert 1948). The Ohm's law analogue describes water flow rate (W, kg s^{-1}) in terms of the difference in water potential between the soil (Ψ_{soil}) and the leaf (Ψ_L):

$$\Psi_{soil} - \Psi_L = (1/K_{soil} + 1/K_r + 1/K_{sh})W \qquad (1a)$$

where K_{soil} is the hydraulic conductance of the soil. It is usually assumed that $K_{soil} \gg K_r$ and K_{sh} except in dry soils so $1/K_{soil}$ can be ignored. Leaf water potential is approximated by:

$$\Psi_L \cong \Psi_{soil} - (1/K_r + 1/K_{sh})W \qquad (1b)$$

Or if we wish to express Eq. 1b in terms of leaf area and average evaporative flux density (E) we have:

$$\Psi_L \cong \Psi_{soil} - (1/K_r + 1/K_{sh})A_L E \qquad (2)$$

This equation can also be rewritten so that root and shoot conductances are scaled to leaf surface areas, i.e., to give leaf-specific shoot and root conductances, K_{sh}/A_L and K_r/A_L, respectively:

$$\Psi_L \cong \Psi_{soil} - [1/(K_r/A_L) + 1/(K_{sh}/A_L)]E \qquad (3)$$

Meristem growth and gas exchange are maximal when water stress is small, i.e., when Ψ_L is near zero. From Eq. 3 it can be seen that the advantage of high K_r/A_L and K_{sh}/A_L is that Ψ_L will be closer to Ψ_{soil}. Leaf-specific stem segment conductivities, K_L, are high in adult pioneer trees, so the water potential drop from soil to leaf is much smaller than in old-forest species (Machado and Tyree 1994). This may promote rapid extension growth of meristems in pioneers compared with old-forest species. In addition, stomatal conductance (g_s) and therefore net assimilation rate are reduced when Ψ_L is too low. During the first 60 days of growth of Quercus rubra L. seedlings, there was a strong correlation between midday g_s and leaf-specific plant conductance, $G = K_p/A_L$, where $K_p = K_r K_{sh}/(K_r + K_{sh})$ (Ren and Sucoff 1995). This suggests that whole-seedling hydraulic conductance is limiting g_s though its effect on Ψ_L. There also is reason to believe that whole-shoot conductance limits g_s in mature trees of Acer saccharum Marsh (Yang and Tyree 1993). Thus, high values of K_r/A_L and K_{sh}/A_L may promote both rapid extension growth and high net assimilation rates in pioneers.

Scaling is always necessary to normalize for plant size. As seedlings grow exponentially in size we would expect an approximately proportional increase in K_r and K_{sh}. Since roots and shoots both supply water to leaves and since an increase in leaf area means an increase in rate of water loss per plant, we would expect K_r and K_{sh} to be approximately proportional to A_L.

We hypothesized that (1) plants experiencing exponential growth in dry matter and leaf area will also exhibit exponential growth of root and shoot hydraulic conductance, (2) root and shoot conductances per unit leaf area ought to be higher in light-demanding versus shade-tolerant species, and (3) some ways of scaling root and shoot conductances to plant size may be more successful than others in showing differences in successional stages as it applies to adaptation to light regimes.

Materials and methods

Plant material and growth conditions

Five species representing a range of successional stages were selected based on the availability of seeds (Table 1). Two pioneer species, *Miconia argentea* and *Apeiba membranacea*, regenerate only under high light conditions in treefall gaps (Brokaw 1987; J. Dalling, unpublished data). *Gustavia superba*, which is intermediate in its light requirements, is most abundant in secondary forest but can persist for at least a year in the forest understory (Sork 1987). Both *Pouteria reticulata* and *Trichilia tuberculata* are shade tolerant.

Seeds of all species were germinated in flats in the 2nd week of August 1994 and transplanted to 2.5-l pots after the emergence of the first mature leaves. Pots were lined with fine plastic mesh screen to prevent roots from emerging from the base of the pots. Soil consisted of a 3:7 mix of washed sand and topsoil from Barro Colorado National Monument (BCNM, 9°7.5′N; 79°52′W) in central Panama. Plants received natural rainfall but were watered as needed, usually three times a week in the dry season; no fertilizer was used. All seedlings were grown in the same screened enclosure on BCNM used in a previous study (Kitajima 1994). The mean daily total PPFD and %PPFD measured on eight consecutive days in 1994 were 6.5 mol m^{-2} day^{-1} and 25%, respectively, in our growth conditions.

Harvests and measurements

Five to six representative seedlings per species were harvested at intervals of 4–7 weeks when plants were 4–16 months old. Root and shoot hydraulic conductances were measured with a HPFM (Dynamax, Houston, Tex.). The HPFM is described in detail elsewhere (Tyree et al. 1993; Yang and Tyree 1994). The theory of HPFM operation when it is attached to roots is discussed in more detail in Tyree et al. (1994, 1995).

Transient measurements of root conductance, K_r, were made with the HPFM, which measures K_r by pushing water from the base of an excised root to the tip (opposite to the normal direction of flow during transpiration). The shoot is excised from the root about 0.02 m above the soil. The HPFM is attached to the cut base of a 1.5- to 6-mm-diameter root system still in the pot with an Omnifit connector (R000451001, Varian Associates, Walnut Creek, Calif.). P_i at the base is increased rapidly from 0 to 0.5 MPa at a constant rate of 3–7 kPa s^{-1} while measuring flow, F, and applied pressure, P_i, every few seconds. The slope of the relationship between F and P_i is taken as K_r. Tyree et al. (1995) have shown linear relationships between F and P_i and good agreement with the K_r measured by the pressure chamber method. After K_r was measured by transient methods, shoot conductance, K_{sh}, was measured by transient and quasi-steady-state methods as described in Yang and Tyree (1994).

Following measurement of K_{sh} and K_r, the leaves were removed and leaf area determined with a Li-Cor 3200 leaf area meter (Li-Cor, Lincoln, Neb.). Soil was washed from the roots. All soil and washing water were passed through a sieve to recover the (rarely) broken roots. Roots were divided into diameter classes, i.e., fine roots (≤2 mm diameter) and coarse roots (>2 mm diameter). The fine and coarse roots, stems, and leaves were dried for >48 h at 60° C and dry weights determined to the nearest 0.1 mg. Root surface areas and lengths were measured with a Delta-T root scanner system (Dynamax) on subsamples of fine roots to obtain a conversion factor between root dry weight and surface area or length. Preparing samples for the root scanner was too time consuming for direct measurement of all root areas and lengths.

Results and discussion

All species experienced exponential growth from age 4 to 16 months when samples were harvested. Typical examples of dry matter and leaf area accumulation are shown in Fig. 1. Values of K_r and K_{sh} also increased exponentially with time (Fig. 2). Since the growth rate of all species was exponential, differences between species
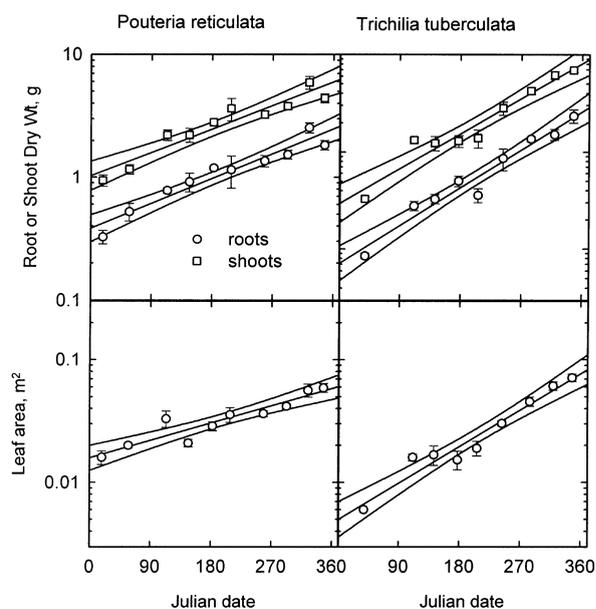
Fig. 1 Typical growth curves showing that growth of *Pouteria reticulata* and *Trichilia tuberculata* was exponential during the period of harvests when plants were 4–16 months old. *Points* are means ($n = 5$–6), *error bars* are SEM (when bigger than the points), *straight lines* are linear regressions of the log-transformed y-values, and *curved lines* are 95% confidence intervals of the regressions

Table 1 Species and species characteristics used in this study. Root categorized by diameter size class where the most frequent diameter is *fine* ≤0.25 mm, *medium* 0.25–0.35 mm, and *coarse* >0.35 mm diameter. All species were germinated in the 2nd week of August 1994. *Gap index* refers to the percentage of recruits 1–4 cm DBH (Diameter at breast height) found in low-canopy sites (<10 m canopy height) in the 50-ha forest dynamics plot on Barro Colorado National Monum. Values ≥12% indicate recruitment patterns skewed towards low-canopy (gap) sites (Weldon et al. 1990)

Species, authority, family	Successional stage	Roots	Gap index
Miconia argentea, (Sw.) DC., Prodr, Melastomataceae	Pioneer	Fine	60.6
Apeiba membranacea, Spruce ex Benth, Tiliaceae	Pioneer	Fine	–
Gustavia superba, (H.B.K.) Berg, Rhizophoraceae	Intermediate	Coarse tap root	55.0
Pouteria reticulata, (Engl.) Eyma, Sapotaceae	Young forest	Medium	23.9
Trichilia tuberculata, (Tr. and Pl.) C. DC., Meliaceae	Old forest	Coarse tap root	14.3

in scaled conductance values are presumed not to be due to limitations imposed by pot size in the discussion that follows.

A statistical analysis of K_r and K_{sh} versus leaf area for each species revealed that root and shoot conductance increased roughly in proportion to leaf area. Plots of K_r/A_L and K_{sh}/A_L versus date of harvest from January to December revealed slopes that were not significantly different from zero. Thus the seedlings maintained a homeostasis in leaf-specific hydraulic conductances.

Ratios of root to shoot dry weight were ≤ 1 in all species (Table 2) with no dependence on age (data not shown). Conversion factors between surface area and dry weight of fine roots were assessed in all species during May and November 1995 and were significantly different in May versus November only for *M. argentea*; values were pooled for all other species (Table 2). The ratio of fine-root surface area to leaf surface area (A_r:A_L) was calculated for all plants harvested in May and November 1995. All values within a species were pooled in Table 2 because A_r:A_L was not significantly different in May versus November. Fine roots accounted for $>95\%$ of the total surface area of seedlings. In *M. argentea* seedlings, root surface areas equaled leaf surface areas; in all other species, root surface areas were 0.12–0.43 times the leaf surface areas. Values of A_r:A_L were higher than previously reported for tropical shrubs and saplings (range: 0.053–0.18; Becker and Castillo 1990); these values were obtained by excavating plants in the field with trowels, fingers, and dandelion diggers, so it is likely that the smallest roots were broken off. We believe we recovered all roots by washing soil from roots into fine sieves.

Since K_r and K_{sh} values increased exponentially during growth, comparisons between species cannot be made with raw data. A suitable means of scaling K_r and K_{sh} to plant size is needed to reveal differences between species that may correlate with light adaptation. The scaling parameter selected may differ depending on the biological question being asked, i.e., physiological questions concerning the mechanism or pathway of transport versus ecological questions related to adaptations to microsites.

A common way of scaling K_r to plant size is to divide K_r values by the surface area of fine roots; in this case we are dividing by the surface area perpendicular to the pathway of water movement to produce a specific conductivity. Implicit in this type of scaling is the assumption that the hydraulic resistance to water flow radially into the root exceeds the hydraulic resistance to water

Fig. 2 Hydraulic conductance of roots (K_r) and shoots (K_{sh}) of seedlings 4–16 months old versus date of harvest. The log-linear increase with time indicates that conductances increase exponentially with time. Species are: *Ma Miconia argentea, Am Apeiba membranacea, Pr P. reticulata, Gs Gustavia superba,* and *Tt T. tuberculata.* Means, errors, *n* and regressions as in Fig. 1

Table 2 Measured root parameters. R:S = root to shoot dry weight ratio, A_r:*FRDW* = fine root surface area per unit fine root dry weight (m^2 kg^{-1}), A_r:A_L = fine root surface area to leaf surface area. Fine roots account for $>95\%$ of all surface area in all species. All values are means $\pm$ SEM for $n = 10$ for R:S and A_r:A_L, and 10–15 for A_r:FRDW. A one-way Tukey test revealed the following significant differences ($P < 0.05$): for R:S *M. argentea* vs. *T. tuberculata* and *G. superba* vs. *A. membranacea, P. reticulata,* and *T. tuberculata*; for A_r:FRDW *M. argentea* and *A. membranacea* vs. all others; for A_r:A_L *M. argentea* vs. all others. Letters *M* and *N* indicate values sampled in May and November, respectively, which were significantly different ($P < 0.05$)

Species	R:S	A_r: FRDW	A_r:A_L
M. argentea	0.532 ± 0.063	$35.1M \pm 1.3$ $21.3N \pm 1.7$	0.972 ± 0.11
A. membranacea	0.467 ± 0.063	23.6 ± 1.3	0.364 ± 0.036
G. superba	0.763 ± 0.082	8.62 ± 0.51	0.193 ± 0.065
P. reticulata	0.392 ± 0.048	11.2 ± 0.6	0.324 ± 0.038
T. tuberculata	0.279 ± 0.017	11.8 ± 3.4	0.200 ± 0.057

flow along the axis of the root. There is reason to believe this assumption is valid (Nobel and Sanderson 1984; Frensch and Steudle 1989; North et al. 1992). Otherwise we would want to divide by the cross-sectional area of the roots. Figure 3A shows values of K_r/A_r for the five species in this study. Data were pooled for the two harvest months since there was no significant difference for the two harvest dates. Values of K_r/A_r differed significantly between a few species, though no pattern with light adaptation (successional stage) was evident, i.e., the two light-demanding species (*M. argentea* and *A. membranacea*) were not distinct from the shade-tolerant species (*P. reticulata*, *G. superba*, and *T. tuberculata*). Another common way of scaling to plant size is to divide K_r by total fine-root length (L). From Fig. 3B it can be seen that the relative ranking of K_r/L is nearly the same as the ranking of K_r/A_r.

The light adaptations (successional stages) more clearly separated when we used $A_r/TRDW$ or $L/TRDW$ to measure the cost of producing roots. The advantage of additional root surface or length per gram is better access to water and mineral nutrient resources in pioneer versus old-forest species. By contrast, the roots of shade-tolerant species are more robust, and presumably less susceptible to damage and predation (cf. Kitajima 1994). Mean values for the two pioneer species were significantly different for the May and November harvests when seedlings were 10 and 16 months old, respectively, and are not pooled in Fig. 3C, D. We tentatively conclude that the advantage gained by more favorable values of $A_r/TRDW$ and $L/TRDW$ in pioneer species may be gradually lost as they age, but more work is needed to confirm this trend.

In Fig. 4A, the root and shoot conductances are scaled by root and shoot dry weights, respectively. In Fig. 4B, the root and shoot conductances are scaled by dividing both by leaf area. In both cases, the adaptive advantages of the pioneer species become evident. All pioneer species differed significantly from the non-pioneer species. Figure 4A, B illustrate two advantages of pioneers versus other species in this study. The higher
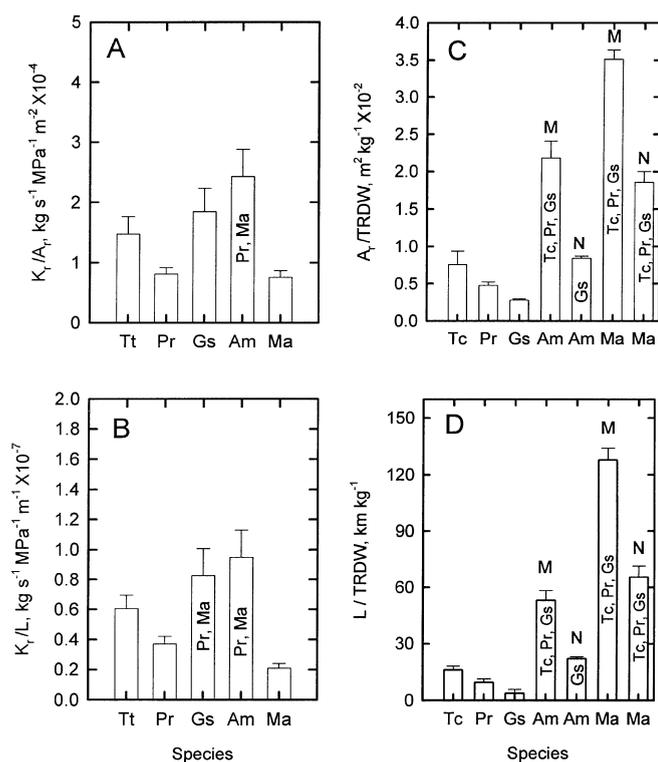
Fig. 3 Different ways of scaling growth parameters: K_r scaled (divided) by fine-root surface area (A_r). (**A**); K_r scaled to fine-root length (**B**); A_r scaled to total root dry weight ($TRDW$ = dry weight of fine plus coarse roots) (**C**); fine-root length (L) scaled to TRDW (**D**); *Error bars* are SEM, n = 5–6 for May or November and 10–12 for pooled data. Data were measured in May and November; when means were not significantly different, values were pooled. Letters *M* and *N* indicated non-pooled data for May and November, respectively, which were significantly different (Tukey test, $P \leq 0.05$). Species abbreviations as in Fig. 2. *Species abbreviations within a bar* indicate which species means are significantly different (Tukey test, $P \leq 0.05$) from the bar bearing the abbreviations
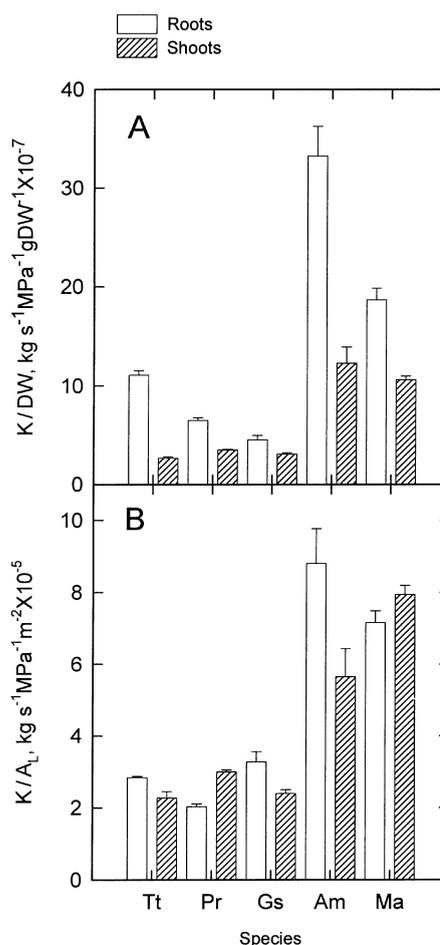
Fig. 4 Hydraulic conductances of shoots and roots scaled to dry weight or leaf area: K_r per unit TRDW and K_{sh} per unit shoot dry weight (**A**); K_r and K_{sh} both scaled to leaf area (A_L) (**B**). *Error bars* are SEM, n = 23–36. Data from all collection dates combined. Species abbreviations as in Fig. 2. Root and shoot means for *Am* and *Ma* were significantly different from corresponding root and shoot means for *Tt*, *Pr*, and *Gs* in both **A** and **B** (Tukey test, $P \leq 0.05$)

values of K_r/A_L and K_{sh}/A_L mean that the pioneer species can maintain less negative leaf water potentials than the other species at any given transpiration rate (see Eq. 3). This might lead to higher rates of extension growth and net assimilation. The higher values of K_r/DW and K_{sh}/DW in pioneers means that pioneers spend less carbon to provide efficient hydraulic pathways than do the other species. Both of these advantages (Fig. 4A, B) mean that pioneers can be more competitive in gap environments than old-forest species.

Although some people may argue that the only valid way of scaling root conductance is by dividing by A_r, we feel there is merit in alternative scaling methods. As stated earlier, we believe that the kind of scaling needed depends on the biological question being asked. Scaling K_r by A_r seems particularly appropriate in the context of physiological questions as in research that concerns the rate and pathway of movement of water and mineral nutrients into roots. Scaling K_r or solute permeabilities to root surface area allows comparison to specific conductances of whole-root surfaces to root surface components such as cell membranes and cell walls that provide parallel pathways for water and solute flow. Our study shows that in an ecological context, alternative scaling factors may reveal light adaptations that are not evident when scaling is by division by A_r or L. Nevertheless, scaling by division of K_r by A_r is highly recommended. In the future we may find two species with identical A_r per unit fine-root dry weight with one having an advantage because of significantly higher K_r/A_r. We need to study more examples before recommending one scaling method over another.

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